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Effects of fertilisation and irrigation on 'foliar afterlife' in alpine tundra

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Abstract

Question: How do increases in soil nutrient and water availability alter the nutrient fluxes through the resorption and litter decomposition pathways and how do they affect litter nutrient pools in a low-productive alpine tundra ecosystem?

Location: An alpine lichen-rich tundra on Mt. Malaya Khatipara in the NW Caucasus, Russia (43°27' N, 41°42' E; altitude 2800 m a.s.l.).

Methods: We conducted a 4-year fertilisation (N, P, N+P, lime) and irrigation experiment, and analysed the responses of nutrient resorption from senescing leaves, leaf litter quality and decomposability of six pre-dominant vascular plant species, total plant community litter production and litter (nutrient) accumulation.

Results: Vascular plant litter [N] and [P] increased 1.5 and 10 fold in response to N and P additions, due to increased concentrations of the nutrients in fresh leaves and unchanged or reduced resorption efficiency. Litter decomposability was not affected by nutrient amendments. Fertilisation enhanced litter production (180%; N+P treatment) and litter accumulation (80%; N+P), owing to tremendously increased production and low decomposability of graminoids. Together with increased litter [N] and [P] this led to great increases in total litter nutrient pools.

Conclusions: Due to increased production of graminoids, nutrients added to the alpine tundra soil were mostly immobilised in recalcitrant, nutrient-rich litter. This suggests that changing species composition in low productive ecosystems may act as an internal buffer mechanism, which under increased soil nutrient availability prevents the community from rapidly acquiring features typical of a high productive ecosystem such as high decomposability and high nutrient availability.

Keywords: Alpine ecosystem; Forb; Graminoid; Litter production; Litter decomposition; Litter quality; Mineralisation; Nutrient addition; Plant growth form; Resorption.

Nomenclature: Vorob'eva & Onipchenko (2001).

Introduction

In many mid-latitude Eurasian mountain ecosystems the availability of nutrients has strongly increased during the past few decades. Global climate change has affected these mountain ecosystems through the retreat of alpine glaciers, increased annual precipitation and temperature increase itself, and this pattern of change is predicted to be accelerated this century (Anon. 2001). As an indirect effect, soil nitrogen availability is set to increase because climate warming may result in faster N mineralisation (Rustad et al. 2001). Moreover, external nitrogen inputs from both NOx and NHy also strongly affect mountain regions of the Northern Hemisphere.

Changes in nutrient and water availability may be particularly important for alpine ecosystems, which exhibit low productivity and strong nutrient (especially nitrogen) limitation (Körner 2003). This is mainly due to the slow litter decomposition and mineralisation (Bryant et al. 1997) caused by a short and cold growing season (Monson et al. 2001). Due to low decomposition rates (Monson et al. 2001; Seastedt et al. 2001) litter forms a substantial part (up to 40%) of the above-ground plant mass (Voronina et al. 1986) and a critical potential source of future carbon and nutrient release to the atmosphere and soil. Yet, little is known about the effects of changes in nutrient and water availability on 'foliar afterlife' processes of alpine plants.

During leaf senescence, nutrients are partitioned between the resorption and the decomposition pathways (Aerts 1997). In the first pathway, nutrients are resorbed from senescing organs and transported to other plant parts where they can be stored and re-utilised (Aerts 1995; Killingbeck 1996). The resorption efficiency (proportion of the maximum foliar nutrient pool resorbed), which is on average 50% for N and 52 % for P, shows no clear response to increased soil fertility (Aerts 1996). Resorption proficiency, defined as the terminal nutrient concentration in senescent leaves (Killingbeck 1996)

(where higher proficiency corresponds to lower nutrient concentrations), is much more responsive to increased nitrogen and phosphorus supply (Chapin & Moilanen 1991; Prescott et al. 1993, 1995; Aerts et al. 2003). Effects of increased water availability on resorption processes have not been investigated yet.

In the decomposition pathway the senesced organs form litter mass that potentially releases carbon and mineral nutrients. The nutrients that are mineralised from the litter can become available to plants again or be taken up by competing micro-organisms (Swift et al. 1979). Low quality litter can inhibit growth, thus playing an important role in competitive plant interactions (Wardle et al. 1996; Bowman et al. 2004). Nutrient amendments lead to increased biomass (Neilsen & Lynch 1998), and litter of fertilised plants is often more nutrient-rich (Arnone & Hirschel 1997; Aerts et al. 2003; van Heerwaarden et al. 2003a). It is not clear yet, however, whether changes in litter quality affect litter decomposition rates (Prescott et al. 1995; Aerts & de Caluwe 1997; Arnone & Hirschel 1997). The effects of moisture have been not studied yet, but high soil moisture can limit carbon and nutrient cycling in cold biomes (Bryant et al. 1997; Monson et al. 2001; Seastedt et al. 2001).

Aerts (1997) suggested that in a low-productivity ecosystem the combination of low litter production (caused by low productivity), high foliar nutrient resorption efficiency and low litter decomposability would lead to a low rate of ecosystem carbon and nutrient cycling. This raises the question how increased availability of nutrients or water affects foliar afterlife processes and thereby ecosystem C and N turnover.

Here we present the first comprehensive assessment of the influence of alleviation of ecological stresses on foliar afterlife properties and processes. Using a 4-year fertilisation (N, P, N+P, lime) and irrigation experiment in an alpine tundra in the Northwestern Caucasus, followed by a one-year screening of litter decomposability we tested the hypotheses that:

1. Litter mass production will be enhanced by increased nutrient or water availability,
2. Increased nutrient or water availability will decrease nutrient (N, P) resorption efficiency,
3. Decomposability of leaf litter will increase in response to increased nutrient or water availability, owing to higher litter nutrient concentrations.

Combining hypothesis 1 and 3, we hypothesise that:

4. There will be little if any response of net litter accumulation on the site during the experimental period.

Material and Methods

Site description

The study site is situated on Mt. Malaya Khatipara at 2800 m a.s.l. in the Teberda Natural Reserve (43°27' N, 41°42' E), in the Northwestern Caucasus, Russia. Mean annual temperature in the area is 1.2 °C and mean July temperature 7.9 °C (Grishina et al. 1986). Annual precipitation is 1400 mm. However, most of the water falls as snow and, due to high wind velocities, is immediately blown away. Therefore, summer soil water shortage is typical of the site.

The vegetation of the site is dominated by fruticose lichens, mainly *Cetraria islandica*, which cover about 50% of the area. The most common vascular plants are *Festuca ovina, Carex sempervirens*, *C. umbrosa, Alchemilla caucasica*, *Anemone speciosa*, *Antennaria dioica* and *Trifolium polyphyllum*. For detailed descriptions of the site and plant community see Onipchenko (1994, 2004) and for vegetation biomass details see Soudzilovskaia et al. (2005).

Fertilisation and irrigation experiment and sampling

In 1999, we assigned 24 plots of 1.5 m × 1.5 m with visually similar vegetation to the following six experimental treatments: control, irrigation (H_2O), nitrogen (N), phosphorus (P), nitrogen + phosphorus (N+P) and lime. The experiment lasted from May 1999 till September 2002. Irrigation was conducted annually during July-August. During July-August mean daily evapotranspiration on the site is ca. 3 mm (Grishina et al. 1986). Every day the precipitation was measured and if the precipitation over a 3-day period did not compensate for water loss due to evapotranspiration, the plots were irrigated accordingly. On average, we added 40 mm/m^2 water per month. This constituted a 150% increase of monthly precipitation. Nitrogen and phosphorus were added annually during 1999-2002 in May, just after snow melt. Nitrogen was added as urea (9 g-N.m^{-2}.a^{-1}), phosphorus as double superphosphate (2.5 g-P.m^{-2}.a^{-1}). Lime additions were performed in order to reduce soil acidity, which can potentially affect N and P availability to plants (Rorison 1980). Lime (52 g-$CaCO_3$.m^{-2}.a^{-1}) was added twice: in 1999 and 2002, just after snow melt. Amounts of nitrogen, phosphorus and lime were chosen to be comparable to the amounts used in other studies of plant community nutrient limitation (e.g. Tilman & Olff 1991; Shaver & Chapin 1995; Seastedt & Lynn Vaccaro 2001).

In order to analyse whether fertilisation treatments affected the total litter production and accumulation, we selected on each plot two subplots measuring 0.25

m by 0.25 m and cut all the fresh and dead plants at a height of 0.1 cm in the first week of August 2002 (the time of peak standing biomass). The collected material was separated into graminoid spp., forb spp., the evergreen shrub *Vaccinium vitis-idaea*, lichens and litter accumulated from the previous years. We estimated above-ground litter production as the sum of the peak above-ground biomass of forbs and graminoids and the estimated litter production of *Vaccinium* (for biomass production by species see Soudzilovskaia et al. 2005). The graminoids and forbs, which die off above-ground completely each year, represent the major part of litter produced in the current year. We estimated annual litter production for *Vaccinium vitis-idaea* by multiplying its actual biomass by annual biomass turnover rate as estimated from literature data (Parsons 1994; Chapin & Shaver 1996). Biomass turnover rate of *Vaccinium vitis-idaea* does not respond to fertilisation (Chapin & Shaver, 1996). Therefore we used the same values of turnover rate for all treatments. Our estimates are not accurate, but since *Vaccinium vitis-idaea* constitutes only about 13% of fresh biomass on control plots and 11%, 8% and 9% of biomass on N, N+P and P fertilised plots respectively (based on data in Soudzilovskaia et al. 2005) we considered them accurate enough for the purposes of this analysis.

We chose the following species for analyses of chemistry and decomposability: the predominant graminoids *Carex umbrosa*, *C. sempervirens*, *Carex caryophyllea* and *Festuca ovina*, and four forbs: *Anemone speciosa, Carum caucasicum*, *Polygonum bistorta* and *Trifolium polyphyllum*. The three morphologically similar *Carex* species: *C. umbrosa*, *C. sempervirens* and *C. caryophyllea*, were pooled as *Carex* spp. During the first week of August 2002, at the peak of the growing season, we collected fresh green leaves with petioles if any. During the first week of September we collected current year leaf litter of the same species. The species litter samples were split into one half used for chemical analysis and subsequent analysis of resorption, and another half used in a litter decomposition experiment. We estimated current year litter N- and P-pools of individual species by multiplying values of species peak biomass (see Soudzilovskaia et al. 2005) by the species litter [N] and [P] (on a leaf mass-basis).

Chemical analysis of fresh leaves and leaf litter

Fresh green leaf and leaf litter samples were air-dried, then oven-dried (60 ºC, 48 h) and analysed for N-, P-, C- and Ca-concentrations. We determined [N] by dry combustion on a Perkin Elmer 2400 CHNS analyser. For determination of [P], samples were acid digested and analysed colorimetrically using the ammonium molybdate method (Murphy & Riley 1962). We determined [Ca] by atomic absorption spectrometry. We found that most of the analysed species had very low (< 1 $mg.g^{-1}$) P concentrations in fresh tissues and even lower in litter, around the detection limit. Because of the high analytical error for those species, we conducted the analyses of P resorption efficiency only for the species that had green leaf [P] higher than 1 $mg.g^{-1}$ in all treatments (*Anemone speciosa* and *Carum caucasicum*).

Analysis of nutrient resorption efficiency

Due to the leaf morphology and chemistry of the species we studied, an accurate estimate of N and P resorption efficiency based on lignin concentrations or leaf area (cf. van Heerwaarden et al. 2003b) was not possible. Therefore, we combined bass-based and Ca-based resorption efficiency estimates, although both methods are suboptimal. Using a mass basis for resorption estimates leads to an underestimation of resorption efficiency owing to resorption of C-rich compounds (Killingbeck 1984; van Heerwaarden et al. 2003b). It is known that Ca is not resorbed due to its immobility in phloem (Lambers et al. 1998). Nevertheless, Ca content is not constant in plant tissue due to leaching (Chapin & Moilanen 1991; Lambers et al. 1998) and accumulation during the growing season (Larcher 2002), and it might be influenced by fertilisation. We compared [Ca] in fresh leaves and in litter at different treatments and found that there was no influence of the treatments on [Ca]. Thus, we concluded that [Ca] in the plants was not influenced by fertilisation and if [Ca] changed during the growing season, these changes were the same in all plots.

Litter decomposition

For a comparative analysis of litter decomposability, we sealed air-dried leaf litter into nylon mesh bags and buried the bags in an outdoor litter bed at the Abisko Scientific Research Station, North Sweden, from mid September 2002 till early October 2003, using an existing litter incubation bed facility (Quested et al. 2003). The climate of the Abisko site, in terms of length of growing season (ca. 4 months), mean temperatures of the growing season (about 9 °C) and low growing season precipitation, is broadly comparable to the litters' site of origin (Anderson et al. 1996; Onipchenko 2004). The set-up of the decomposition experiment generally followed that of Quested et al. (2003). Sub-samples of the initial material were dried (48 h at 60 °C) in order to determine the ratio between air-dry and completely dry material. We put 50-300 mg pre-weighed air-dried leaf litter material of each species in each litter bag (1 mm mesh, except for *Festuca ovina* litter, 0.3 mm mesh). The

litter bed was divided into four 70 cm × 70 cm compartments each 10 cm deep and litter samples of each species were put randomly in the litter bed compartments, so that each compartment contained only one litter bag from each experimental treatment replication. We filled the litter bed with litter taken from nearby birch heath woodland and incubated the litter bags approximately 2 cm below the surface. After one year of incubation, we retrieved the litter, dried it (48 h at 60 °C) and calculated percentage mass loss on a dry mass basis.

Statistical analysis

The effects of the treatments on resorption efficiency was analysed by two-way ANOVAs with treatment and species as independent variables and mass-based or Ca-based resorption efficiency as a dependent variable. If the ANOVAs showed a significant treatment x species interaction, we ran per-species one-way ANOVAs with treatment as independent factor followed by a Dunnett *post-hoc* test. A log-transformation was applied to data throughout in order to improve normality.

We applied one-way ANOVA with treatments as independent factors, followed by Dunnett's post-hoc test to analyse the changes in the litter mass production induced by fertilisation. To detect whether forbs and graminoids differed in their litter production response to fertilisation, we ran a two-way ANOVA with treatment and plant type as independent factors. Since the analyses showed a significant plant type × treatment interaction, we ran separate one-way ANOVAs for graminoid and forb biomass with treatment as independent factor, followed by Dunnett's *post-hoc* test. The changes in litter mass accumulated from the previous years were analysed by one-way ANOVA with treatments as independent factors, followed by Dunnett's *post-hoc* test.

To analyse the effects of the treatments on litter quality (N, P, C concentrations, and N/P ratio) and current year litter N- and P-pools we ran two-way ANOVAs with species and treatment as independent variables. If the ANOVAs showed a significant treatment × species interaction, we ran per-species analyses with treatment as independent factor followed by a post-hoc test. If the data for individual species had a normal distribution, or could be normalised by log or square root transformation, we ran an ANOVA followed by Dunnett's *post-hoc* test. If species data could not be normalised, we ran a Kruskal-Wallis test followed by a Mann-Whitney test. We did not have enough data to analyse changes in amount of P accumulated in *Polygonum bistorta*.

Treatment effects on litter mass loss were analysed using two-way ANOVA with species and treatment as independent variables. As this analysis showed no significant effect of treatment, but a significant difference between species, we performed an additional nested two-way ANOVA in order to find out whether forbs differed from grasses in litter mass loss. In order to improve normality we applied arcsine-square root transformation to these data.

To determine whether the difference in decomposition rate was caused by litter quality (which changed in response to fertilisation) or by other species traits (not analysed within this study) we ran ANCOVAs with species as an independent factor and a respective chemical parameter (N, P, C concentration, N/P ratio) as a covariate. The latter data were log-transformed in order to improve normality.

Results

We found no response to lime amendments in any of the analysed ecosystem parameters. Similarly, there were no responses to the irrigation treatment. Therefore, these factors will not be further discussed.

Resorption efficiency

Ca-based nitrogen resorption efficiency estimates ranged from 40 to 85 % among species and treatments (Fig. 1). For N-resorption efficiency, Ca-based data indicated a marginal treatment effect ($F = 1.98$, $P = 0.090$), a marginal difference among species ($F = 2.08$, $P = 0.076$) and a significant species × treatment interaction ($F = 4.35$, $P < 0.001$). Mass-based N-resorption estimates were in almost all cases considerably lower, ranging from 30 to 70% (Fig. 1). Mass-based N-resorption data also indicated a marginal treatment effect ($F = 2.27$, $P = 0.054$), but a significant difference among species ($F = 9.88$, $P < 0.001$) and no treatment × species interaction ($F = 1.13$, $P = 0.330$). Taking into account these partly conflicting results we ran one-way ANOVAs per species. Both one-way ANOVAs conducted on Ca-based and on mass-based data indicated a significant treatment effect for *Trifolium polyphyllum* (c. 40% lower in N-treatment, Ca-based ANOVA: $F = 7.75$, $P = 0.002$; mass-based ANOVA: $F = 4.77$, $P = 0.008$) (Fig. 1).

Ca-based P-resorption efficiencies also ranged between 40 and 80% (Fig. 2). The Ca-based data indicated a significant effect of treatment ($F = 3.73$, $P = 0.01$), no difference between species ($F = 2.60$, $P = 0.12$), and no treatment × species interaction ($F = 1.48$, $P = 0.23$). As with N, mass-based P-resorption efficiencies were consistently lower than Ca-based resorption efficiencies, ranging from 15 to 70% (Fig. 2). The mass-based data also indicated a significant treatment effect ($F = 6.22$, $P = 0.001$), no difference between species ($F = 1.08$, $P = 0.31$) but a significant species × treatment interaction

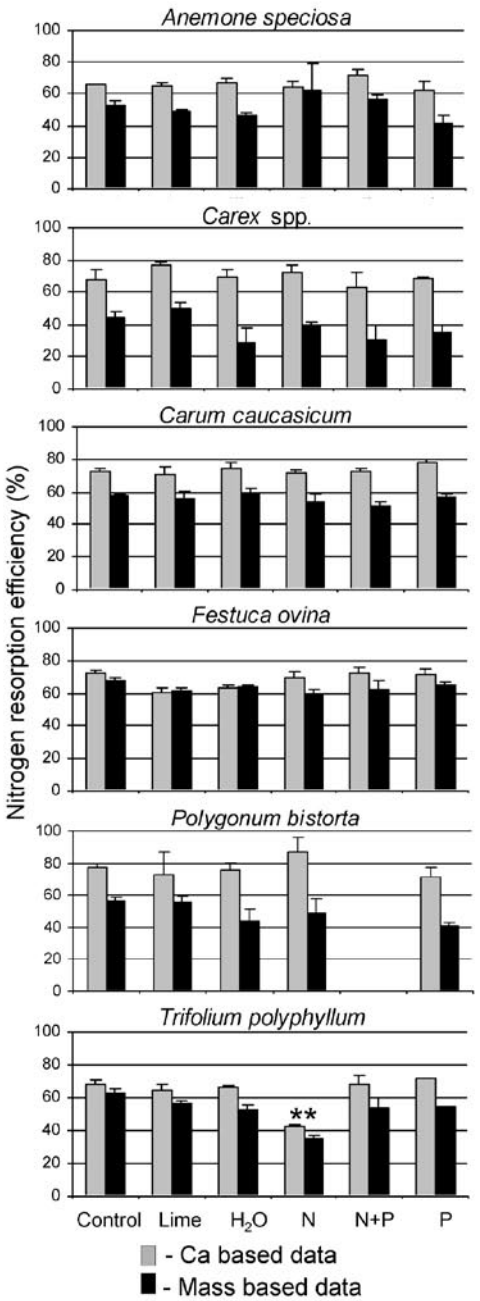

Fig. 1. Response of nitrogen resorption efficiency (mean ± SE, $n = 4$) to experimental treatments: N (9 g-N.m^{-2}.a^{-1}), P (2.5 g P.m^{-2}.a^{-1}), N+P (9 g N.m^{-2}.a^{-1} + 2.5 g P.m^{-2}.a^{-1}), Lime – lime addition during the first and last year of the experiment (52 g-lime.m^{-2}.a^{-1}), H_2O: annual irrigation during July and August. Only for *T. polyphyllum* there was a significant difference from the control in the N-treatment. * indicates significant differences from control treatment. ** = $P < 0.01$ (Dunnett's test).

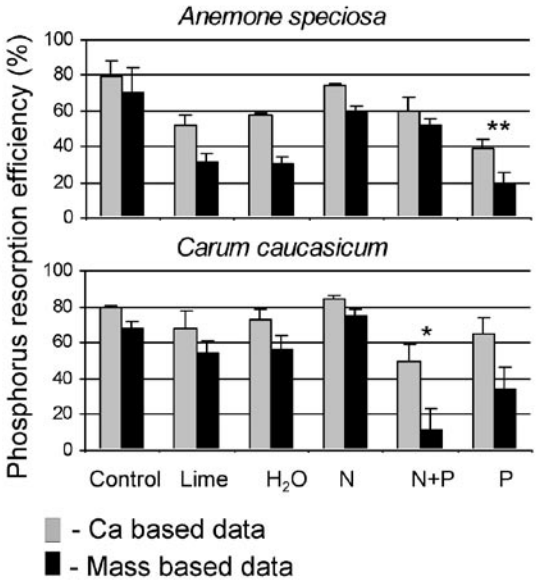

Fig. 2. Response of phosphorus resorption efficiency (mean ± SE, $n = 4$) to experimental treatments. See Fig. 1 for treatments details. * indicates significant differences from control treatment. * = $P < 0.05$, ** = $P < 0.01$ (Dunnett's test).

($F = 3.40$, $P = 0.016$). Subsequent one-way ANOVAs on both Ca based and mass-based data, indicated marginally significant treatment effects for both *Anemone speciosa* (Ca based ANOVA: $F = 4.56$, $P = 0.011$; mass-based ANOVA: $F = 4.18$, $P = 0.022$) and *Carum caucasicum* (Ca based ANOVA: $F = 2.85$, $P = 0.048$; mass-based ANOVA: $F = 6.09$, $P = 0.002$), due to a significant decrease in P-resorption efficiency for *Anemone speciosa* in response to P-additions and for *Carum caucasicum* in response to N+P-additions (Fig. 2).

Current year litter production and accumulation of litter from the previous years

The estimated above-ground litter production was 110 g.m^{-2} on the control plots and 310 g.m^{-2} on N+P plots (ANOVA: $F = 15.7$, $P < 0.001$; Dunnet test $P < 0.001$). The estimated above-ground litter production of graminoids and forbs was respectively 330% (ANOVA: $F = 11.5$, $P < 0.001$; Dunnett test: $P < 0.001$) and 100% (ANOVA: $F = 3.96$, $P = 0.013$; Dunnett test: $P = 0.017$) higher on N+P treated plots in comparison with the control (Table 1). Total longer-term accumulated above-ground litter mass was 80% higher (ANOVA: $F = 5.63$, $P = 0.003$; Dunnett test: $P = 0.003$) on N+P treated plots than on the control (Fig. 3).

Table 1. Mean (± SE, $n = 4$) potential aboveground litter production of forbs and graminoids at the fourth year of fertilisation and their 1-year litter mass losses in a decomposability assay. * indicates significant difference from control treatment (Dunnett's test). * = $P < 0.05$, *** = $P < 0.001$. Litter mass loss was not influenced by any of the treatments.

	Treatment	Litter production $g.m^{-2}$	Litter mass loss (%)
Forbs	Control	63 ± 7	82 ± 6
	Ca	68 ± 15	82 ± 4
	H_20	52 ± 8	85 ± 3
	N	95 ± 16	86 ± 4
	NP	123 ± 17*	88 ± 4
	P	74 ± 9	83 ± 5
Graminoids	Control	42 ± 7	36 ± 2
	Ca	54 ± 6	35 ± 4
	H_20	35 ± 9	39 ± 6
	N	85 ± 21	39 ± 7
	NP	179 ± 30***	42 ± 8
	P	53 ± 5	38 ± 4

Changes in litter chemistry and litter nutrient pools

Responses of litter N-, P- and C-concentrations to fertilisation are shown in App. 1. Litter [N] and [P] (i.e. N and P resorption proficiency), significantly increased in response to addition of the respective nutrient (treatment effects $F = 23.9$, $P < 0.001$ and $F = 81.1$, $P < 0.001$, respectively). The increase of litter [N] was 20-120% in response to N or N+P fertilisation. Remarkably, [N] of *Polygonum bistorta* increased significantly in response to P-additions. The P-additions resulted in great increases of [P], ranging from 280 to 1800%. *Festuca ovina* showed a threefold stronger increase of [P] in response to the N+P treatment than in response to P treatment alone. Changes in N/P ratio were mostly driven by the dramatic increases of [P]. Carbon concentrations were not altered by fertilisation.

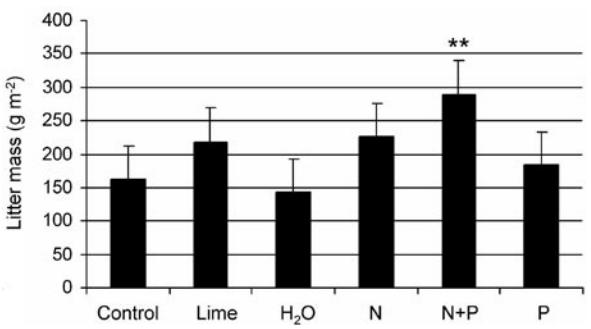

Fig. 3. Above-ground accumulated litter mass (mean ± SE, $n = 4$) in response to experimental treatments. See Fig. 1 for treatment details. * indicates significant differences from control treatment. ** = $P < 0.01$ (Dunnett's test).

Nitrogen and phosphorus additions caused overall increase of the litter pools of the respective nutrients (N pool, treatment effect: $F = 8.08$, $P < 0.001$; P-pool, treatment effect: $F = 30.1$, $P < 0.001$), although at the species level there was considerable variation of litter nutrient pools in different treatments. Whilst all individual species increased the litter N-pool (1.4-7.4 fold) in response to N and to N+P additions (the latter except for *Trifolium polyphyllum*), only in *Carex* spp. and in *Festuca ovina* there was a significant increase for this parameter (Fig. 4a). The amount of N stored in leaf litter of *Carex* spp. was 720 and 740% higher on N and N+P treated plots than on the control (for both N and N+P treatments, $P = 0.029$). The litter N pool of *Festuca ovina* was 700% higher on N+P treated plots than on the control ($P = 0.017$).

Additions of P and N+P caused 3-12 and 3-50 fold increases of litter P-pool in the species analysed, in spite of rather large variances at the species level (Fig. 4b). Remarkably, *Trifolium polyphyllum* accumulated more P at P-fertilised plots than at N+P fertilised plots, although the 1200% increase was only marginally significant owing to large variance ($P = 0.056$). *Carex* spp. and *Festuca ovina* marginally significantly increased the litter P-pool in response to both P and N+P treatments: for *Carex*: P-treatment: $P = 0.050$, N+P treatment: $P = 0.034$; for *Festuca*: P-treatment: $P = 0.021$, N+P treatment: $P = 0.021$. The litter P-pool in *Carum caucasicum* increased only in response to N+P treatment ($P = 0.034$), while *Anemone speciosa* and *Trifolium polyphyllum* did so only in response to the P-treatment (for *Anemone*: $P = 0.044$).

Comparing species, *Carex* and *Festuca* had the largest litter N- and P-pools on N+P treated plots (N-pool: 0.9 and 0.6 $mg.m^{-2}$, respectively; P-pool: 0.11 and 0.09 $mg.m^{-2}$, respectively). On N-treated plots *Carex* had the largest litter N-pool (0.9 $mg.m^{-2}$), while, in spite of an increase of [N], the pool of *Festuca* was only 0.1 $mg.m^{-2}$, similar to pools of other plants. Similarly, on P-treated plots *Carex* had the largest P-pool, while the pool of *Festuca* was within the range measured in other plants (0.01 $mg.m^{-2}$).

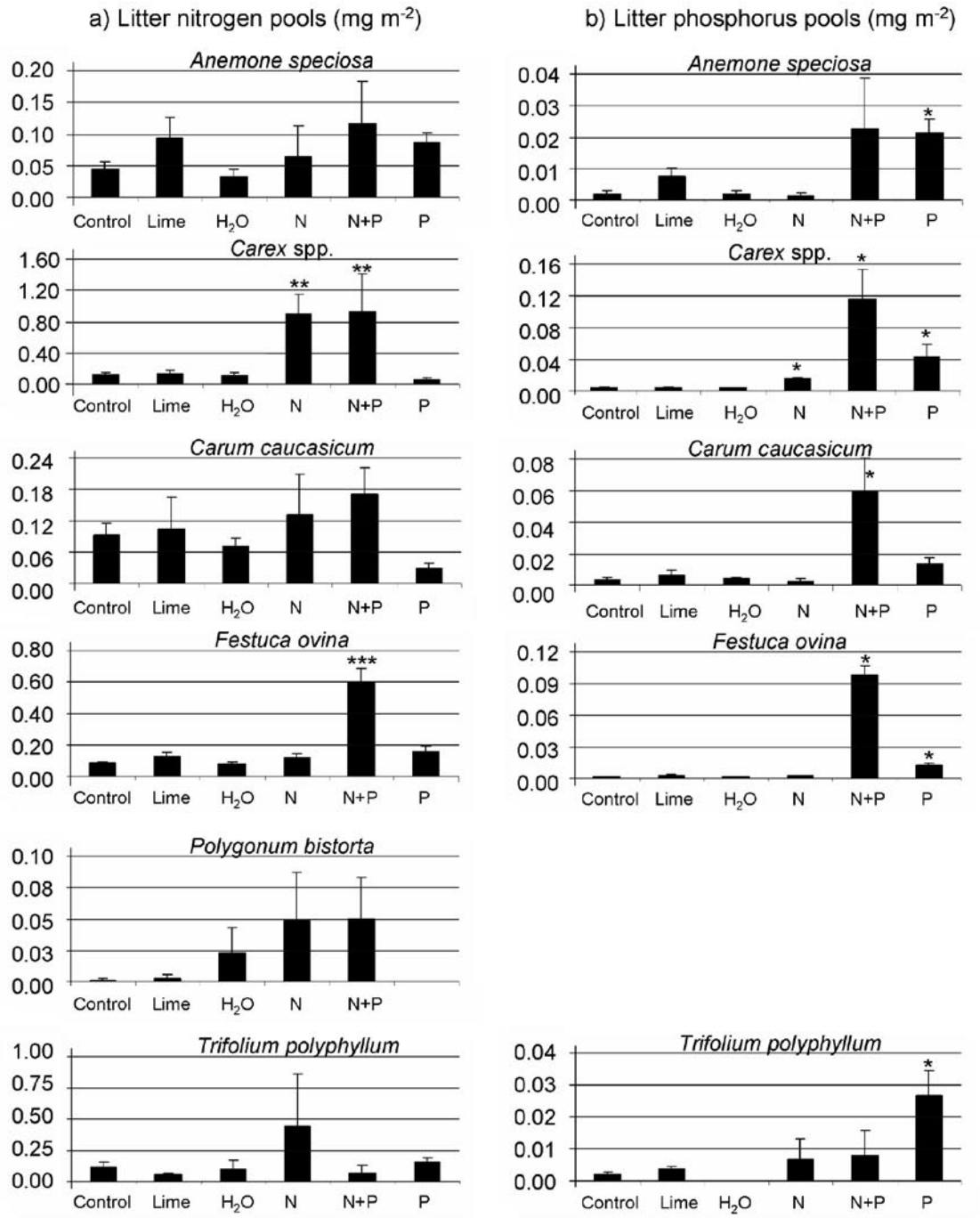

Fig. 4. Current year litter (**a**) nitrogen and (**b**) phosphorus pools of individual species (mean ± SE, $n = 4$) in response to experimental treatments. See Fig. 1 for treatment details. * indicates significant differences from control treatment. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$ (Dunnett's or Mann-Whitney test). Note the different scales on the Y-axes.

Changes in litter decomposability

In the controls, one year litter mass loss varied considerably among species ($F = 204$, $P < 0.001$) with the lowest value for *Festuca ovina* (31%) and the highest value for *Anemone speciosa* (95%) (App. 2). Averaged over the growth forms, the forb species decomposed more than twice as fast as the graminoid species (nested ANOVA, growth form effect: $F = 986$, $P < 0.001$) (Table 1). We found no significant effects of fertilisation treatments on litter mass loss, neither significant species by treatment interaction effects.

Relation between litter chemistry and decomposability

ANCOVAs run on species, chemical traits (N-, P- and C-concentration and N/P, C/N and C/P ratios) and mass loss indicated no effect of chemical traits on mass loss but a highly significant ($F > 35$, $P < 0.001$ in all cases) difference between species in their decomposition rate (see also above). C/N ratio measured in litter from control plots was a barely significant predictor of litter mass loss at the species level ($R^2 = 0.56$, $F = 5.11$, $P = 0.087$, $n = 6$).

Discussion

Experimental design

Resorption efficiency and litter decomposability generally did not show significant responses to experimental nutrient or water amendments. We think that this is less likely, but cannot exclude that this might be caused by the constraints of our experimental design, including only four replicate plots for each combination of treatment and species. Also, our experimental design was not fully factorial so that we may have missed interactions between irrigation, lime additions and nutrient additions.

Resorption efficiency

Both Ca-based and mass-based methods used for the analysis of resorption led to comparable results. Our resorption percentages are within the range reported for other alpine plants, which generally have rather high resorption efficiency (Monson et al. 2001), both for forbs and graminoids (N: 40-75% and P: ca. 50%). N- and P-resorption efficiencies did not differ between the graminoids and forbs analysed, nor did they support the hypothesis of an overall decrease in nutrient resorption efficiency after fertilisation and irrigation. This is in agreement with previous findings (Aerts 1996). However, P-resorption efficiency was reduced for both species analysed, although only significantly so in one of the P-amendment treatments per species. It has been suggested that at P-poor sites resorption efficiency of P decreases after P-additions (Chapin & Moilanen 1991; Rejmánková 2001). The reduced P-resorption efficiency in our experiment is, thus, consistent with the low concentration of soil phosphorus at this experimental site (Makarov 1995; Vertelina et al. 1996). Alpine plants are often strongly N-limited (Körner 2003). Nevertheless, the N-additions did not alter N-resorption efficiency for most of the species analysed within our experiment. This contradicts findings of van Heerwaarden et al. (2003a), who reported a general trend of decreased N-resorption efficiency after fertilisation of an N-limited sub-arctic bog. Aerts (1996) stated in his review that in 63% of the cases, N-resorption was not influenced by N-fertilisation and in 32% it was reduced, while for P the respective values were 57% and 35%. This review concerned mostly trees and evergreen shrubs. Our findings suggest that also for forbs and graminoids no clear-cut pattern can be found in the relation between site fertility and nutrient resorption efficiency.

Soil moisture plays an important role in nutritional processes of alpine plants (Bowman 1994; Fisk et al. 1998). However, the absence of any response in resorption efficiency to irrigation suggests that soil moisture does not control leaf or, consequently, litter quality in the alpine tundra (see also Bowman et al. 1995; Soudzilovskaia et al. 2005). Such an apparent lack of water limitation is probably a consequence of physiological adaptations to water shortage, such as low leaf water potential and low leaf conductance (Oberbauer & Billings 1981). Similarly, the reduction of soil acidity, which may affect N- and P- availability to plants (Rorison 1980), did not influence resorption efficiency in our lime addition treatment.

Decomposition

Contrary to our hypothesis, leaf litter decomposability was not affected by increased nutrient or water supply in spite of increases in litter [N] and [P] in our study. Increases of leaf litter [N] and [P] concentrations after additions of the respective nutrients have also been reported by many other authors (Prescott et al. 1993; Arnone & Hirschel 1997; van Heerwaarden et al. 2003a). This is consistent with the observation that plants growing on richer soils generally have higher litter nutrient concentrations (Chapin & Moilanen 1991; Killingbeck 1996). When different species are compared, litters with higher [N] and especially [P] often decompose faster (e.g. Seastedt 2001; Rejmánková 2001; McGroddy et al. 2004). These reports correspond with previous evidence of slower decomposability of graminoids in comparison

with forbs (Cornelissen 1996; Cornelissen & Thompson 1997; Quested et al. 2003), since graminoids usually also have lower litter nutrient concentrations than forbs. Our data also show that graminoids decompose 2-3 times slower than forbs.

Many experiments have shown that increased nutrient supply does often not lead to an increased litter decomposability, despite increases in litter nutrient concentrations – e.g. Prescott et al. (1993) for *Pseudotsuga* forest, Aerts & de Caluwe (1997) for *Carex* species in temperate bogs, Arnone & Hirschel (1997) for alpine grassland, Aerts et al. (2003) for temperate grassland; but see van der Putten et al. (1997) for a counter example. Our experiments indicate no influence of greater nutrient supply on litter decomposability either. Despite that, after fertilisation, poorly decomposable graminoids like *Festuca ovina* and *Carex* spp. increased their [N] and [P] to a level comparable with N and P concentrations of highly decomposable forbs like *Anemone speciosa* or *Carum caucasicum* under ambient conditions (App. 1).

Earlier studies have shown that leaf structure and toughness play an important role in decomposability (Gallardo & Merino 1993; Pérez-Harguindeguy et al. 2000). Cornelissen & Thompson (1997) suggested that lower tensile strength explains greater decomposability of forbs in comparison with graminoids. We propose that high decomposition rates of species that exhibit high N- and P-litter concentration are not caused by high N- and P-concentrations *per se*, but by other plant traits (e.g. low toughness or low lignin or cellulose concentrations) that coincide with high nutrient concentrations. This is consistent with the suites of traits generally found in functional groups of plant species (Chapin et al. 1993; Díaz et al. 2004).

Litter production and litter accumulation

We found a strong increase in annual above-ground litter production and subsequent litter accumulation on N+P fertilised plots. Nutrient additions are known to promote shifts in species composition of arctic and alpine tundra, mainly as a result of increased dominance of graminoids in the total community vascular plant biomass (Henry et al. 1986; Fox 1992; Bowman et al. 1993; Van Wijk et al. 2003). In agreement with this, the total graminoid production increased fourfold in response to N+P fertilisation, while the total production of forbs increased only twofold (Table 1). The increased litter production, especially of graminoids, in combination with unchanged litter decomposability (see above) explain the observed litter accumulation on N+P fertilised plots.

Nutrient flux: consequences for the ecosystem

In general, nutrient amendments increase both biomass and nutrient concentration in plants, thus increasing the amounts of nutrients accumulated in the ecosystem (Bowman 1994; Press et al. 1998; Güsewell et al. 2003). In another study at the same site (Soudzilovskaia et al. 2005) we showed that after the fourth year of fertilisation, the total above-ground vascular plant N-pool increased 2.8-fold on N-treated plots and 3.2 fold on N+P plots. Similarly, the total above-ground vascular plant P-pool increased 8.3-fold on P-plots and 13.2-fold on N+P plots. However, in the present study we found that resorption efficiency did either not change or decreased after fertilisation. Thus, the nutrient concentration of litter increased very strongly. Together with the increased litter production, this has led to a strong increase in the amount of nutrients stored in current year litter, especially of graminoids. Nevertheless, potential decomposition of the litter was not increased in response to the nutrient additions. Therefore, the most conspicuous effect of the nutrient additions was a drastic increase in litter production and litter accumulation. Thus, in this alpine ecosystem, increased nutrient availability promotes the accumulation of nutrients within the growing layer of slowly decomposing, mostly graminoid litter, at least in the short- to medium term (4 years). However, in the long term, even at low mineralisation rates, the total pool of (accumulated) nutrients turned over per unit area would probably increase.

Our results suggest that changing species composition of a low productive ecosystem may act as an internal buffer mechanism, owing in our case to negative feedback from low litter decomposability of grasses compared to forbs. Under increased soil nutrient availability this feedback prevents the community from acquiring features typical of a high productive ecosystem such as high decomposability and high nutrient availability. Owing to this internal buffer mechanism alpine ecosystems show a delayed nutrient turnover response to increased nutrient inputs by immobilising the nutrients in slowly decomposable although nutrient-rich litter.

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